RESULTS

Bird Detections

Observers recorded 16,850 individuals representing 34 bird species (Appendix 1) during 1,565 point-count visits distributed over 153 sampling stations placed among 57 cottonwood patches. Among these, 5,587 individuals were recorded during 511 visits in grazed areas; 3,171 individuals during 337 visits at recreational campgrounds; and 8,092 individuals in 717 visits at unmanaged sites. Most (82%) of the 34 species were Neotropical migratory landbirds (Appendix 1). Evaluating cumulative number of species over area revealed that detections of 32 species (94% of the species analyzed for this study) had accumulated by the time patch size reached 3 ha.

Overall species richness was similar among land-use types, with all 34 species recorded in grazed and unmanaged sites, and 32 species detected at recreational campgrounds (Eastern Kingbird and Yellow-billed Cuckoo were not recorded at campgrounds). Species diversity and evenness also were similar among land-use types (grazed H'=2.83, E=0.80; recreation H'=2.86, E=0.83; unmanaged H'=2.84, E=0.80). For cottonwood patches sampled in all four years (1991-1994), species turnover did not significantly differ among land uses [$\bar{x}$ ($\pm$1SE) for grazed [N=10]=1.53(0.04); recreation [N=5]=1.63(0.06); unmanaged [N=21]=1.61(0.03); df=2, F = 1.45, p = 0.25], where the numbers represent the average change in species composition from one year to the next recorded within a single cottonwood patch.

Land use had a very strong effect on mean number of species and individuals detected per point count visit (Table 3, Fig. 2). No overall size effect was found for number of species or individuals [$\bar{x}$($\pm$1SE) for number of species detected in large=4.12(0.14); medium=3.69(0.18); small=4.43(0.14) patches; and for number of individuals detected in large=11.15(0.32); medium=10.02(0.36); small=11.42(0.35) patches]. However, there was a significant interaction effect between land use and patch size. A significant year effect was found, while there was no interaction effect between year and the main effects of land use and patch size (Table 3). Tests of paired comparisons among land uses showed that mean number of species per point count visit was significantly different for all land uses, with species numbers lowest in recreation campgrounds (Fig. 2A). Mean number of individuals also was significantly reduced in recreation areas compared to grazed or unmanaged lands (Fig. 2B). Results of the multiple comparisons (an evaluation of the interaction between land use and patch size) revealed that mean number of species and individuals did not significantly differ between large-recreation patches and unmanaged areas, and large-recreation patches and the larger patch sizes of grazed lands (Fig. 3A, 3B).

Table 3a, 3b. Differences among effects of land use, patch size and year on (a) mean number of species per point count visit, and (b) mean number of individuals per point count visit.

a. Mean number of species per point count visit

ANOVA for effects	SS	df	F	*p*
Main effects				
Land use	30.41	2	10.97	<0.001
Patch size	1.87	2	0.67	0.51
Year	14.20	3	3.42	0.02
Interactions				
Land use*Patch size	20.09	4	3.62	0.01
Land use*Year	2.16	6	0.26	0.95
Patch size*Year	4.77	6	0.57	0.75
Land use*Patch size*Year	7.24	10	0.52	0.87

b. Mean number of individuals per point count visit

ANOVA for effects	SS	df	F	*p*
Main effects				
Land use	63.97	2	4.91	0.01
Patch size	26.32	2	2.02	0.14
Year	227.65	3	11.66	<0.001
Interactions				
Land use*Patch size	94.91	4	3.64	0.01
Land use*Year	29.18	6	0.75	0.61
Patch size*Year	19.54	6	0.50	0.81
Land use*Patch size*Year	15.14	10	0.23	0.99

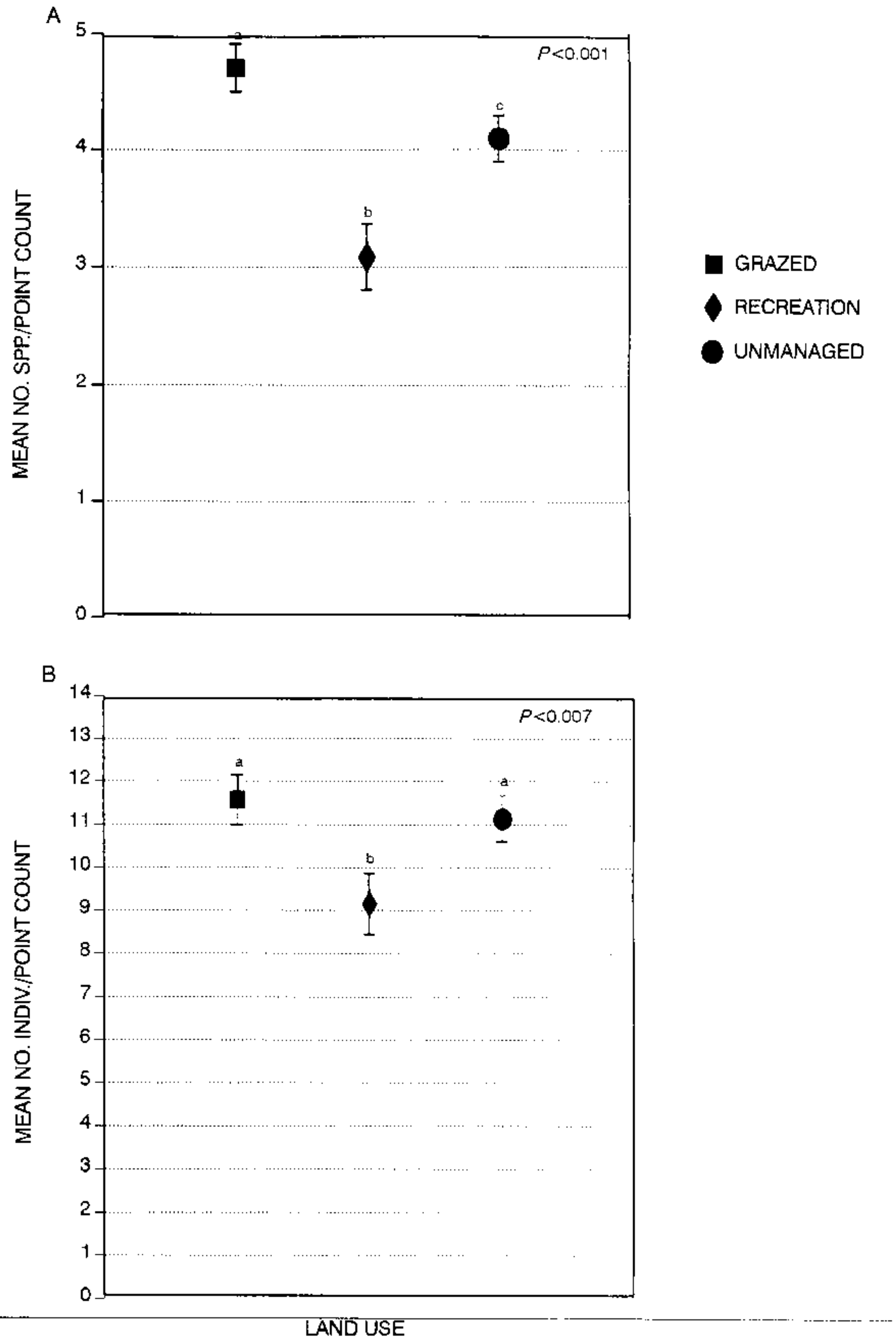

Fig. 2. Mean number of species (A) and individuals (B) detected per point count survey in each land-use type, averaged over all years and all patch sizes. Vertical lines represent ± SE. In each graph, different lower-case letters indicate that corresponding means are significantly different at $p \leq 0.05$.

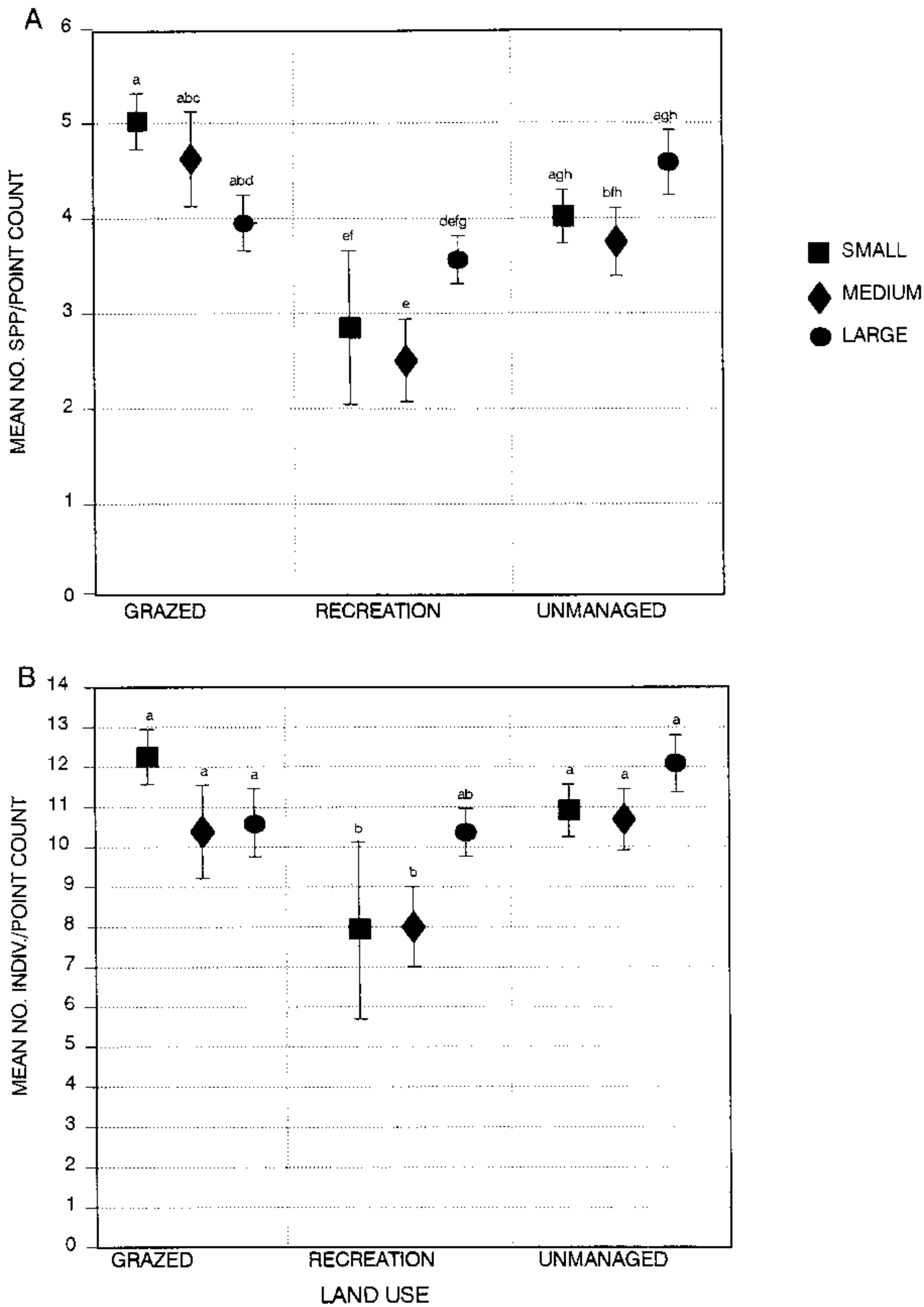

Fig. 3. Mean number of species (A) and individuals (B) detected per point count survey by land use and patch size, averaged over all years. Vertical lines represent $\pm$ 1 SE. In each graph, different lower case letters indicate that corresponding means are significantly different at $p \leq 0.05$.

Among years, 1991 generally had fewer species and individuals per point count visit compared to all other years (Fig. 4). Intensity of use by cattle or recreationists may have differed in some years but I did not quantify the change in use from one year to the next. During 1991 in unmanaged sites, however, species numbers and combined-individual abundances were significantly different from other years except for species richness in 1994. This suggests that a factor other than changes in land-use intensity may have been responsible for the reduced numbers of species and individuals during 1991 (e.g., local inclement weather).

Species were grouped by nest layer based on the placement of their nests (ground, shrub, or canopy; see Appendix 1) to test for differences in their relative abundance among land uses and patch sizes (Fig. 5A). Results suggested some differential land-use and patch-size effects among the three groups of nest layers (Table 4). Ground-nesting and canopy-nesting species were primarily responsible for the land-use effect, and ground nesters only for the patch-size effect (Table 4, Fig. 5). No effect was significant for shrub nesters, although their relative abundance was lowest in recreation areas (nonsignificant p=0.11). Using these results for prediction, ground nesters should respond negatively to grazing and camping activities, canopy nesters should respond positively to grazing (at least over the short-term), and shrub nesters should tend to respond negatively to recreational and grazing activities.

Species were also grouped by nest type as either cavity or open-cup nesters (Appendix 1) to test for differences in their relative abundance among land uses. Open-cup nesters included a group of 26 species that varied greatly in their life histories and habitat requirements (e.g., American Crow and Yellow Warbler); however, the cavity-nesting group consisted of only eight species that did not vary as widely in life history, habitat use, or taxonomy (included four woodpecker species in the family Picidae). Results indicated a significant overall land-use effect on cavity and open-cup nesting species (Wilk's lambda = 0.76; $F(94,106) = 3.99$; $p = 0.005$). By examining the univariate ANOVAs and mean values for relative abundances of cavity and open-cup nesters, the differential response to land uses appeared largely due to cavity-nesting species, whose relative abundances were highest in grazed areas and lowest in recreation campgrounds (Table 5).

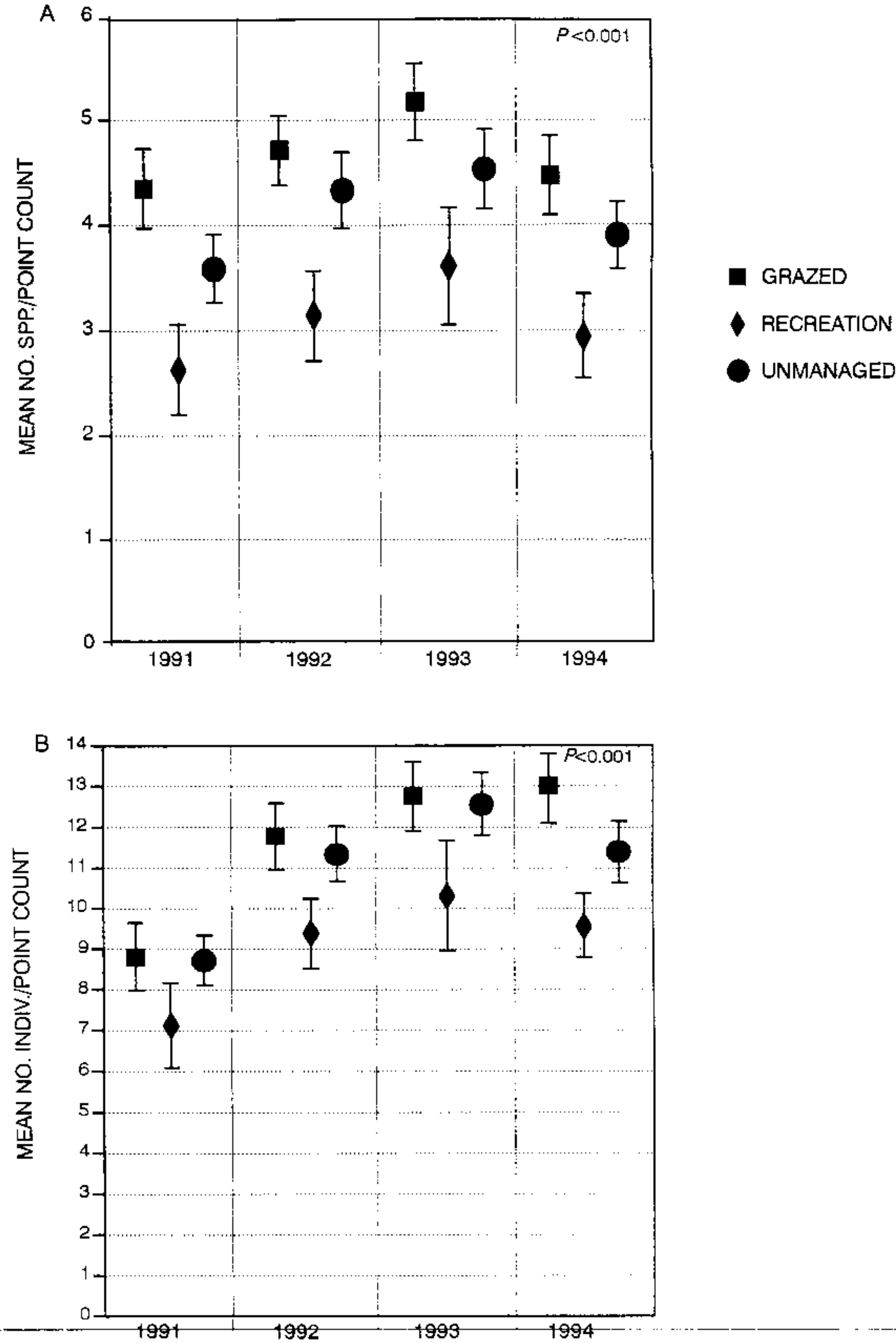

Fig. 4. Mean number of species (A) and individuals (B) detected per point count survey by year and land use, averaged over all patch sizes. Vertical lines represent ± 1 SE.

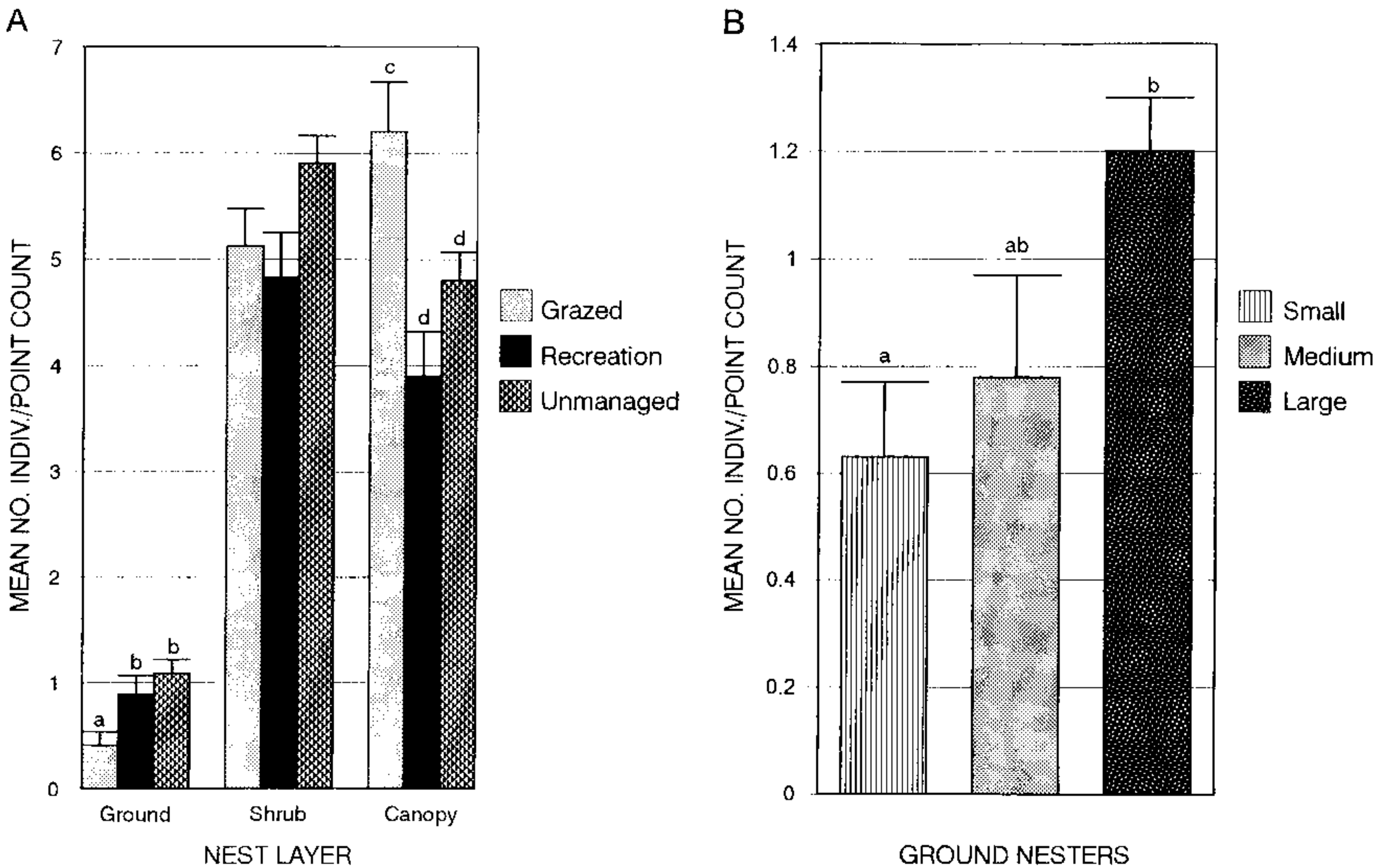

Fig. 5. Mean number of individuals by nest layers within each land-use type (A) and mean number of individuals for ground-nesting species within patch sizes (B). Vertical lines represent 1 SE. Within each nest layer, different lower-case letters indicate that corresponding means are significantly different at $p \leq 0.05$.

Table 4. Effects of land use and patch size on the abundance of species grouped by nest layer, based on the placement of their nests on either the ground, in shrubs, or in the canopy (see Appendix 1). ANOVA results are presented to aid in interpreting dependent variables from suggestive MANOVAs.

MANOVA effect	Wilk's Lambda	F	Num df	Den df	*p*
Land use	0.64	3.89	6	92	0.002
Patch size	0.65	3.69	6	92	0.003
Land use*Patch size	0.65	1.80	12	122	0.06

ANOVAs for effects	SS	df	F	*p*
Ground Nesters				
Land use	1.24	2	5.51	0.007
Patch size	1.27	2	5.67	0.006
Land use*Patch size	0.94	4	2.11	0.10
Error	5.38	48		
Shrub Nesters				
Land use	0.33	2	2.27	0.11
Patch size	0.02	2	0.15	0.86
Land use*Patch size	0.10	4	0.03	0.85
Error	3.52	48		
Canopy Nesters				
Land use	0.93	2	6.85	0.002
Patch size	0.35	2	2.59	0.09
Land use*Patch size	0.59	4	2.14	0.09
Error	3.28	48		

Over half (17 or 53%) of the 30 bird species analyzed suggested some differential effects of land use and patch size, and/or the interaction between the two main effects (Table 2). Compared to unmanaged sites with little or no use by cattle or recreationists, relative abundance per point count visit for eight species decreased in grazed lands (Black-capped Chickadee[BCCH], Veery[VEER], Yellow Warbler[YEWA], Yellow-breasted Chat [YBCH], Black-headed Grosbeak[BHGR], Lazuli Bunting[LZBU], Fox Sparrow [FOSP], and Song Sparrow[SOSP]). Abundance for eight species decreased in recreation campgrounds (Mourning Dove[MODO], Black-capped Chickadee[BCCH], House Wren[HOWR], Veery[VEER], Yellow Warbler[YEWA], Lazuli Bunting [LZBU], American Goldfinch[AMGO], and Fox Sparrow[FOSP]). In contrast, some species increased in grazed areas (Mourning Dove[MODO], Dusky Flycatcher [DUFL], Black-billed Magpie[BBMA], House Wren[HOWR], and European Starling [EUST]), and in recreation campgrounds (Warbling Vireo[WAVI]) compared to unmanaged areas. For most species showing significant patch-size effects, relative numbers were highest in large patches (Gray Catbird[GRCA], Warbling Vireo [WAVI], Yellow Warbler[YEWA], Black-headed Grosbeak[BHGR], and American Goldfinch [AMGO]).

Table 5a, 5b. Effects of land use activities on the relative abundance of species grouped by nest type (cavity or open-cup nesters). For descriptive statistics in each nest type category, different letters indicate that corresponding means are significantly different ($p \leq 0.05$).

a. Descriptive Statistics

Nest Type	Grazed Mean($\pm$SE)	Recreation Mean($\pm$SE)	Unmanaged Mean($\pm$SE)
Cavity	3.28 ($\pm$0.42)a	1.70 ($\pm$0.29)b	2.26 ($\pm$0.17)b
Open	7.95 ($\pm$0.44)	7.76 ($\pm$0.70)	9.20 ($\pm$0.39)

b. Mean number of detections per point count visit

ANOVAs for effects	SS	df	F	p
Cavity Nesters				
Land use	19.94	2	5.39	0.007
Error	99.91	54		
Open-cup Nesters				
Land use	24.68	2	2.98	0.06
Error	223.74	54		

Results of the logistic regression suggested differential area effects on 10 species, depending on land use activities (Table 6). European Starling and Song Sparrow were the only species with probability of occurrences that were consistently and significantly highest in small patches within all land uses. Four species (Warbling Vireo [WAVI], Veery [VEER], Black-headed Grosbeak [BHGR], and Gray Catbird [GRCA]) that had no overall area relationship when land uses were combined, showed an area effect (i.e., increased probability of occurrence with increased patch size) in recreation sites and sometimes in grazed lands. Five species (American Goldfinch [AMGO], Yellow Warbler [YEWA], Veery [VEER], Black-headed Grosbeak [BHGR], and Gray Catbird [GRCA]) were unaffected by patch size in unmanaged areas, but showed significant area effects in grazed and/or recreation sites. Probability of occurrences for Northern Orioles and Black-billed Magpies were significantly highest in small patches of grazed areas, yet in unmanaged lands their probabilities were highest in large patches. Maybe results for these two species are due to chance effects, given the large number of statistical comparisons.

Habitat

Vegetation was measured at three layers: ground, shrub/subcanopy, and canopy. An overall land-use effect was found for three ground cover variables of bare, shrub, and herb (Wilk's Lambda = 0.63; $F(6,92) = 4.01$; $p = 0.001$) (Fig. 6), an overall patch size effect (Wilk's Lambda = 0.63; $F(6,94) = 4.02$; $p = 0.003$), but no interaction effect between land use and patch size. Percentage of bare ground and herbaceous cover increased with grazing and recreational uses, whereas shrub cover decreased with these same land-use activities (Fig. 6). Percentage bare ground [$\bar{x}(\pm 1SE)$ for large=9.02(2.02); medium=6.66(2.37); small=10.77(2.53) patches] and herbaceous cover [$\bar{x}(\pm 1SE)$ for large=19.37(1.80); medium=18.37(2.62); small=30.09(3.70)] also increased in small patches compared with medium and large patches. Percentage of ground covered by logs and litter did not differ significantly among land uses (Fig. 6) or patch sizes.

Densities of woody stems of various sizes were estimated within the shrub/subcanopy layer (Fig. 7). MANOVA results indicated an overall land-use effect on their densities (Wilk's Lambda = 0.60; $F(12,86) = 2.11$; $p = 0.02$), primarily due to reductions of smaller diameter stems in areas managed for grazing and recreation (Fig. 7a). There was no patch size effect ($p = 0.21$) or land use/patch size interaction ($p = 0.37$) on overall stem densities.

Stem densities were also recorded by plant species (Table 7). Overall stem densities of the most abundant woody plant species were apparently affected by land use activities and patch sizes (Table 7a). Changes in stem densities associated with land use effects were primarily due to reductions of alder, birch, and dogwood in grazed lands compared to unmanaged areas (Table 7b). Silverberry and Western Clematis were the only species with significantly different densities within patch size classes. Densities of both species were higher in large forest patches.

Table 6. Effect of patch size and land use on species detection. Values are probabilities of detecting species in cottonwood forest patches of various sizes within three land uses. *P*-values associated with each land use and the chi-square statistic for testing the relationship between species' frequency of occurrence and forest patch size of all land uses were estimated by logistic regression analysis. Species are ordered from those with the strongest positive relationship with patch size to those with the most negative relationship. Patch sizes are S=small (<1-3 ha); M= medium (>3-10ha); and L=large (>10-204 ha). *P*-value for chi-square test statistic: $*p<0.05$, $**p<0.01$, $***p<0.001$; NS=nonsignificant.

	Probability of Detecting Species by Cottonwood Patch Size												
	Grazed				Recreation				Unmanaged				All Land Uses
Species	S	M	L	p	S	M	L	p	S	M	L	p	χ^2
AMGO	0.46	0.46	0.57	<0.001	0.26	0.26	0.34	0.07	0.54	0.54	0.56	0.64	11.57*
MODO	0.30	0.30	0.31	0.83	0.09	0.10	0.16	0.03	0.15	0.20	0.40	<0.001	10.05**
YEWA	0.92	0.92	0.94	0.08	0.75	0.83	0.96	<0.001	0.94	0.94	0.96	0.15	6.47*
DUFL	0.09	0.09	0.08	0.46	0.02	0.02	0.05	0.01	0.02	0.02	0.06	<0.001	3.67*
WAVI	0.37	0.38	0.39	0.52	0.59	0.61	0.70	0.01	0.35	0.38	0.50	<0.001	3.10(NS)
VEER	0.12	0.12	0.20	<0.001	0.15	0.17	0.26	0.004	0.37	0.37	0.34	0.51	0.02(NS)
BHGR	0.14	0.14	0.14	0.89	0.11	0.12	0.23	<0.001	0.20	0.20	0.20	0.94	0.13(NS)
GRCA	0.10	0.10	0.07	0.14	0.06	0.08	0.18	<0.001	0.12	0.12	0.15	0.20	0.32(NS)
NOOR	0.34	0.33	0.23	0.002	0.13	0.14	0.21	0.01	0.28	0.30	0.41	<0.001	4.29*
BBMA	0.26	0.23	0.09	<0.001	0.21	0.19	0.11	0.01	0.10	0.11	0.16	0.03	13.24***
EUST	0.32	0.32	0.14	<0.001	0.09	0.08	0.04	0.05	0.19	0.17	0.12	0.04	17.74***
SOSP	0.38	0.37	0.14	<0.001	0.63	0.60	0.34	<0.001	0.55	0.53	0.46	0.02	73.12***

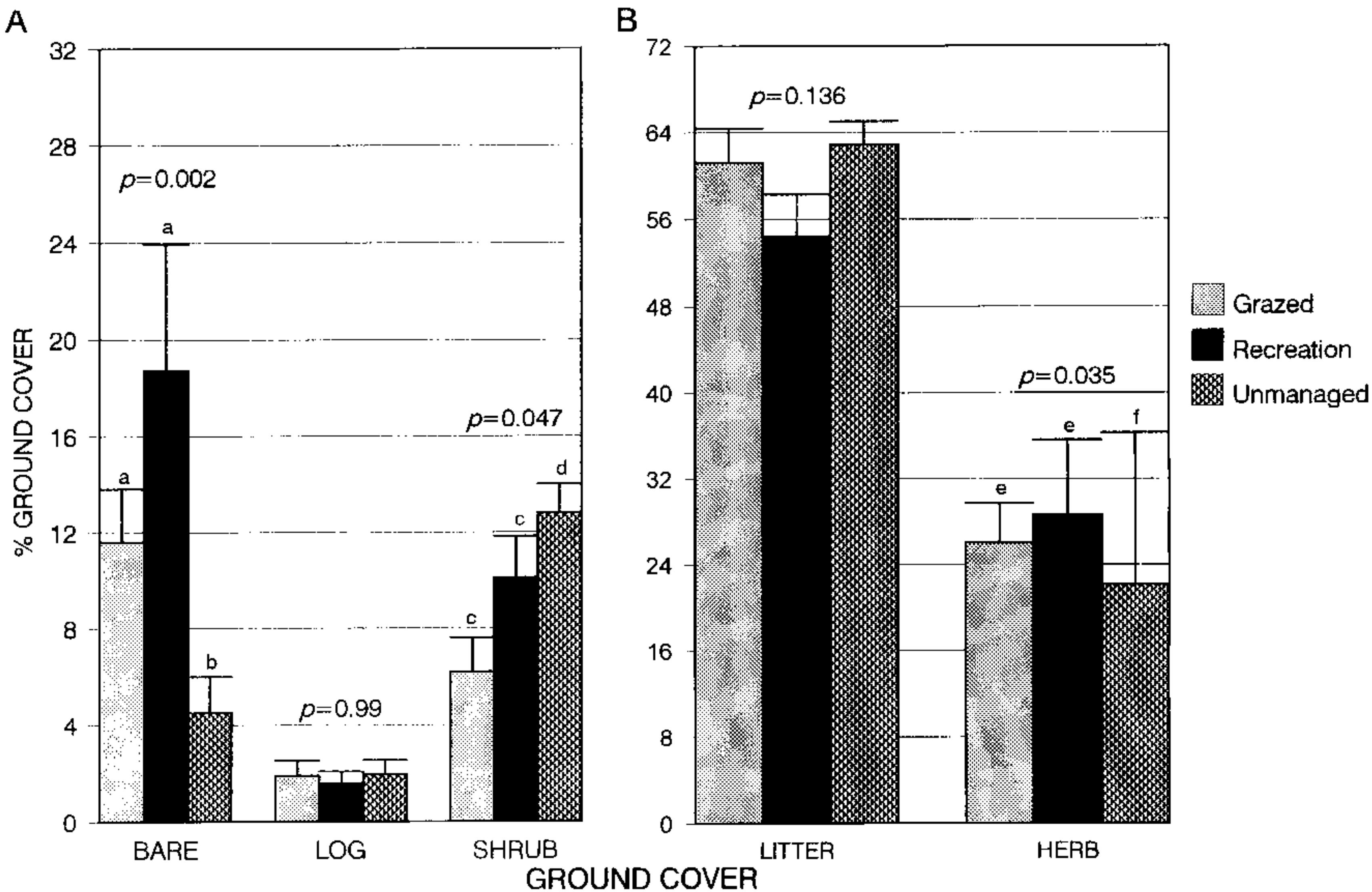

Fig. 6. Mean percentage of five ground cover categories within each land-use type. Vertical lines represent 1 SE. Within each ground cover category, different lower-case letters indicate that corresponding means are significantly different at $p \leq 0.05$.

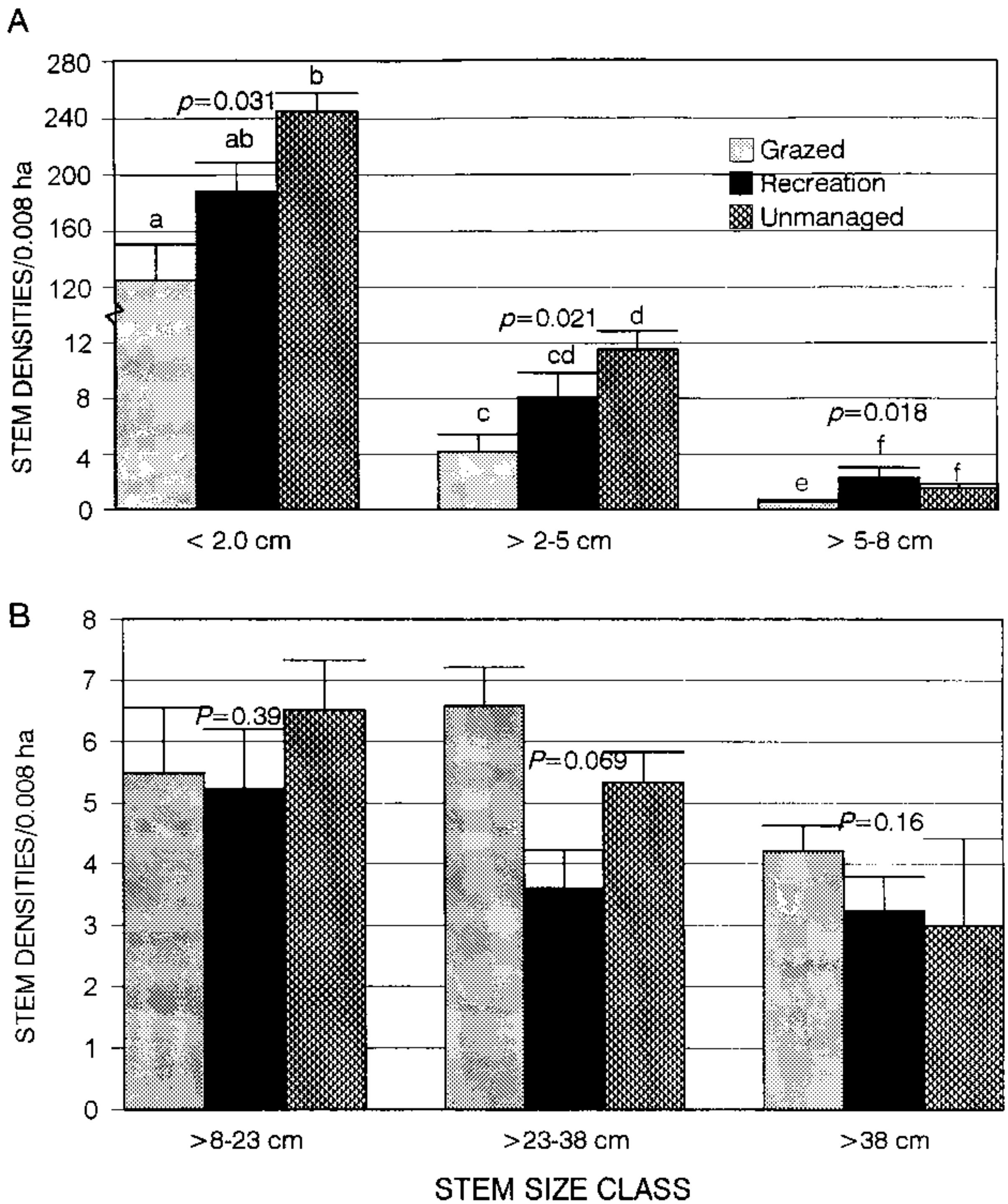

Fig. 7. Average stem densities for small stems (A) per 5-m radius (0.008 ha) sampling station, and large stems (B) per 11.3-m radius (0.04 ha) sampling station within each land-use type. Vertical lines represent 1 SE. Within each stem size class, different lower-case letters indicate that corresponding means are significantly different at $p \leq 0.05$.

Table 7a, 7b. Summary statistics, ANOVA, and MANOVA results for overall stem densities reported for the most abundant woody plant species by land use and patch size.

a. Mean (± 1 SE) and ANOVA results for stem densities of all sizes combined, averaged per 0.04 ha sampling station.

	Land Use				Patch Size			
Species	Grazed	Recreation	Unmanaged	*P*-value	Small	Medium	Large	*P*-value
Thin-leaved Alder *Alnus incana*	0.29(0.29)a	2.77(1.65)ab	3.81(1.32)b	0.03	1.48(0.58)	5.23(2.64)	1.53(0.68)	NS
Water Birch *Betula occidentalis*	2.95(1.75)a	45.62(12.20)b	12.29(3.74)a	<0.001	8.33(3.49)	17.62(9.67)	22.24(5.72)	NS
Western Clematis *Clematis ligusticifolia*	41.39(11.63)	72.84(24.93)	55.24(12.13)	NS	32.90(11.05)a	79.24(19.79) ab	68.81(11.25)b	0.004
Red-stemmed Dogwood *Cornus stolonifera*	42.47(10.89)a	79.55(19.37)ab	110.35(11.12)b	0.03	66.95(12.95)	98.81(14.88)	90.74(13.11)	NS
Douglas Hawthorne *Crataegus douglasii*	1.99(0.94)	1.29(0.45)	2.26(1.44)	NS	1.55(1.34)	2.11(1.14)	2.80(0.89)	NS
Silverberry *Elaeagnus commutata*	11.11(5.41)	11.36(6.87)	11.99(2.25)	NS	6.16(2.09)a	5.84(2.42)a	28.18(6.70)	<0.001
Rocky Mountain Juniper *Juniperus scopulorum*	1.95(0.66)	2.80(0.99)	2.40(1.23)	NS	1.32(0.44)	1.40(0.53)	4.97(2.16)	NS
Narrowleaf Cottonwood *Populus angustifolia*	23.56(4.09)	19.72(3.65)	16.43(1.27)	NS	20.52(3.18)	19.21(2.29)	18.07(1.73)	NS
Willow species *Salix* spp.	10.79(2.54)	23.09(8.53)	21.56(3.72)	NS	14.29(3.21)	24.07(5.04)	19.27(5.39)	NS

b. MANOVA on average stem densities

MANOVA	Wilk's Lambda	F	Num df	Den df	*p*
Land use	0.44	2.27	18	80	0.01
Patch Size	0.38	2.81	18	80	0.01
Land use*Patch Size	0.44	1.04	36	151.64	0.42

Minimal differences in percent canopy coverage were found among land uses (Fig. 8a), but overall canopy increased significantly with decreasing patch size (Fig. 8b). Of the eight plant species whose canopy reached the overstory [listed in decreasing order of canopy coverage: narrowleaf cottonwood, red-stemmed dogwood, water birch, willow spp., thin-leaved alder, chokecherry, Rocky Mountain juniper, and silverberry] no individual plant species had a significant canopy increase in small patches or significant changes among land uses.

Vegetation characteristics of the ground and shrub layers were significantly correlated with abundance of ground and shrub nesting birds, respectively (Table 8). Significant negative correlations were found between abundance of ground-nesting species and percentage of bare ground, and between ground nesters and percent canopy coverage. Significant positive correlations were found between shrub nesters, shrub cover, and shrub densities. Ground nesters also were positively correlated with shrub densities. No significant correlation was found between percentage of canopy cover and abundance of canopy-nesting birds. Ground- and shrub-nesting species showed significant positive correlations, whereas a significant negative correlation was found between ground and canopy nesters.

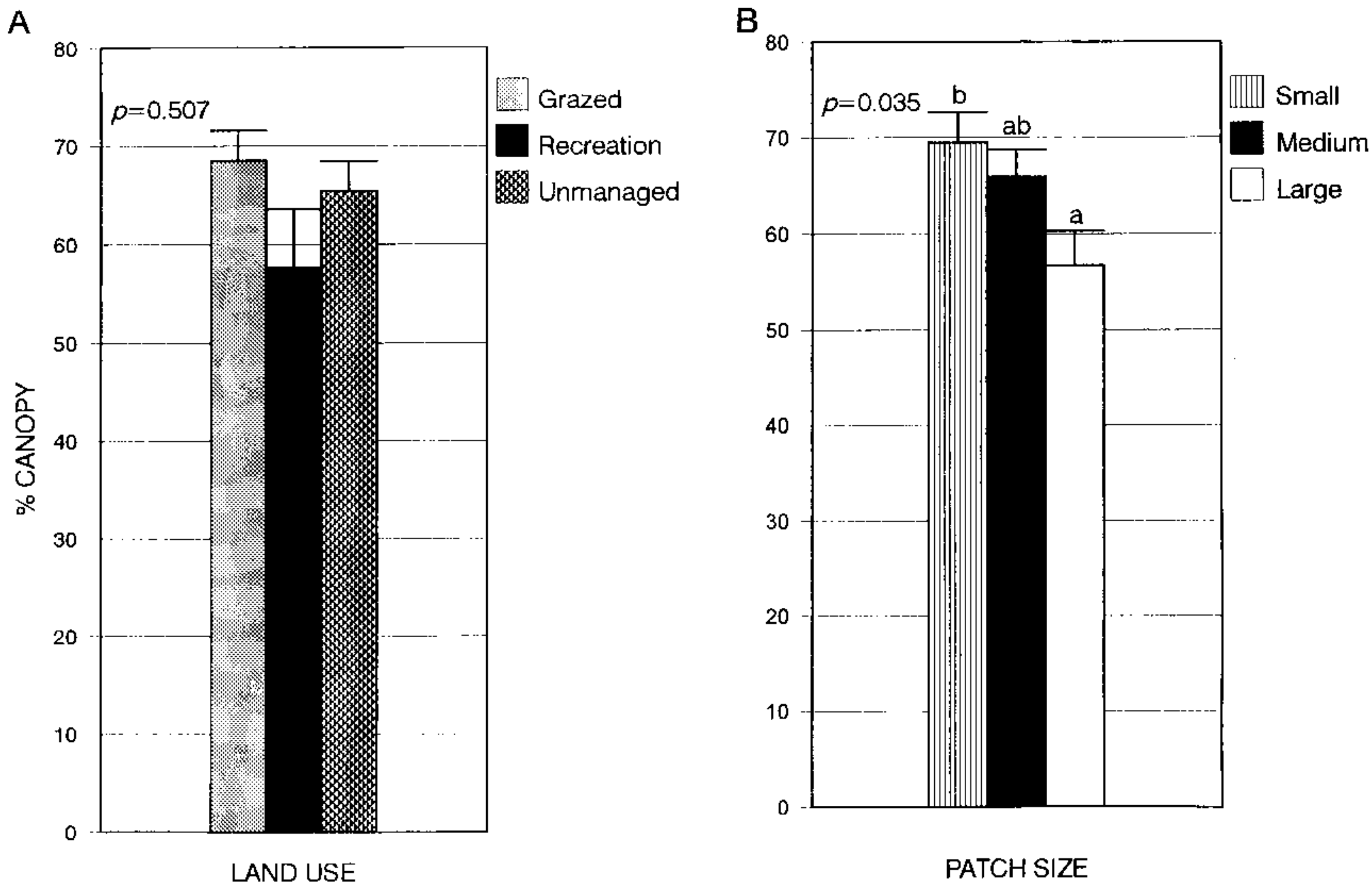

Fig. 8. Mean percentage of canopy cover in each land-use type (A) and patch-size class (B). Vertical lines represent 1 SE. Within each graph, different lower-case letters indicate that corresponding means are significantly different at $p \leq 0.05$.

Table 8. Correlation analysis of relative abundances of species grouped by nest layer (ground, shrub, canopy) and vegetation structural characteristics by layer (ground cover, shrub cover and densities, canopy cover) per sampling station. Spearman correlation coefficients are listed with statistical significance indicated by * $p \leq 0.05$, ** $p < 0.01$, *** $p < 0.001$.

	Ground Nesters	Shrub Nesters	Canopy Nesters	%Bare Ground	%Shrub Cover	Shrub Stem Densities (≤ 2.5 cm)	Shrub Stem Densities (> 2.5 - 5 cm)
Shrub Nesters	0.33 *						
Canopy Nesters	-0.27 *	0.07					
% Bare Ground	-0.30 *	-0.36 **	0.05				
% Shrub Cover	0.24	0.40 **	-0.08	-0.33 *			
Shrub Stem Densities (≤ 2.5 cm diameter)	0.34 **	0.25*	-0.14	-0.51 *	0.64 ***		
Shrub Stem Densities (>2.5 - 5 cm diameter)	0.54 ***	0.48 ***	-0.37 **	-0.44 ***	0.48 ***	0.43 ***	
% Canopy	-0.28 *	-0.11	0.21	0.09	0.03	-0.26	-0.12